



To warm on the rocks, to cool in the wind: Thermal relations of a small-sized lizard from a mountain environment

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ARTICLE INFO

Keywords:

Ectothermy
Thermal biology
Thermal ecology
Tropiduridade
Eurolophosaurus nanuzae

ABSTRACT

Rising temperatures accompanying global climate change are expected to affect mountain lizards. Therefore, basic information on how these ectotherms deal with their thermal environment is important for further management. We conducted a field study to evaluate how body temperature of the small-sized mountain lizard *Eurolophosaurus nanuzae* relates to the thermal environment. After capture, the body temperature of the lizards was measured immediately, quickly followed by the substrate and air temperatures, wind intensity, and solar radiation at the capture locations. Linear relationships showed that the body temperature of individuals was positively related to rocky substrate temperatures but negatively related to wind speed. However, air temperature and solar radiation were unrelated to body temperature. Although the substrate is an important heat source for *E. nanuzae*, in an open environment it can reach temperatures up to 10 °C above the maximum body temperatures of lizards, and can thus be a low-quality thermal substrate. However, individuals seemed to use wind as a cooling source to counterbalance the risks of overheating from high substrate temperatures. As the montane environment that *E. nanuzae* inhabits seems to have hotter temperatures than those preferred by the species, lizards should benefit from the cooling winds to keep their body temperature at appropriate levels. Different to previous studies that evaluated wind effects on body temperatures of lizards, our results showed that winds seemed to promote thermoregulation for *E. nanuzae*.

1. Introduction

Maintaining body temperature within a limited range favours the performance and fitness of animals. Ectotherms depend on external heat resources, which are used to thermoregulate, to maintain their body temperature within a narrow range (Angilletta, 2009). Among lizards, most are able to effectively regulate their body temperatures when active (e.g. Vitt et al., 1996; Hatano et al., 2001). This is achieved using a set of behaviours involving the selection of appropriate heat sources (Gifford et al., 2012; Block et al., 2013), the adjustment of body postures, positioning according to the source and intensity of heat from the environment (Goller et al., 2014). A failure in thermoregulation or an unavailability of optimal thermal sites might increase the risks of lizards cooling or overheating. This can compromise an animal's metabolism that can ultimately cause death (Huey and Kingsolver, 1989). Therefore, lizards have to actively search for and select optimal thermal microhabitats to maintain their body temperatures (e.g. López-Alcaide et al., 2017).

Lizard body temperatures are frequently related to local abiotic

factors such as substrate and air temperatures (Kiefer et al., 2005; Hatano et al., 2001), wind speed (Maia-Carneiro et al., 2012), and solar radiation (Goller et al., 2014). Body temperatures can also vary between the sexes (Block et al., 2013; Maia-Carneiro and Rocha, 2013), and these sexual differences can be attributed to differential use of the environment by males and females, imposed by ecological or social selective pressures (e.g. Gilbert and Lattanzio, 2016). Body size (or body mass) can also affect the body temperature of lizards, and when there is sexual dimorphism for body size, intersexual variation in body temperature may relate to size differences (Maia-Carneiro and Rocha, 2013). In addition, the thermal environment of high-elevation habitats is known to constrain the thermal behaviour of lizards, leading to shifts in the frequency of basking, and it also restricts the total time available for daily activities (Hertz and Huey, 1981; Ortega et al., 2016b; Alés et al., 2017).

The intricate relationship between the body temperatures of lizards and environmental factors put these animals among the most vulnerable to climate change. Indeed, there is evidence that global warming is affecting such animals (Huey et al., 2012; Telemeco et al., 2016;

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<https://doi.org/10.1016/j.jtherbio.2018.07.003>

Received 7 November 2017; Received in revised form 5 July 2018; Accepted 9 July 2018

Available online 10 July 2018

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Sinervo et al., 2018), which might ultimately lead to species extinction (see Gunderson and Leal, 2016; Sinervo et al., 2010). Risks related to climate change can drastically affect reptiles from mountain environments as this type of habitat is known to present low environmental temperatures (e.g. McCain, 2010). Therefore, mountain lizards are expected to be more affected by rising temperatures as they tend to be cold specialists (Ortega et al., 2016a). Nevertheless, the lack of information regarding the thermal biology of lizards inhabiting Neotropical mountain environments can hamper the management of populations in a scenario of warming temperatures. This fact is especially concerning considering that lizards are poorly represented in the protected areas around the world (Roll et al., 2017).

The lizard *Eurolophosaurus nanuzae* (Rodrigues, 1981) is a small-sized (i.e. average body-size of 50 mm) saxicolous species restricted to the mountaintops (between approximately 1000 and 1400 m a.s.l.) of the ridges of the meridional portion of the Espinhaço Mountain Range, Brazil (Passoni et al., 2008). Although there are differing vegetational formations in the highlands of Espinhaço (see Fernandes, 2016), the species is only found in rocky field habitats. Whilst there are some studies dealing with the ecology of the species (e.g. Galdino and Van Sluys, 2011; Galdino et al., 2006, 2003), the thermal biology of this small-sized montane lizard species remains, to the best of our knowledge, unstudied. Herein, we present basic information on the thermal biology of *E. nanuzae* from a montane environment. Specifically, we ask: Does body temperature differ between the sexes? Is the body temperature of *E. nanuzae* affected by the substrate and air temperatures, solar radiation, and wind speed? Does body mass relate to the body temperature of these lizards?

2. Materials and methods

2.1. Study site

The study was conducted in the Serra do Cipó district, Santana do Riacho Municipality, located in the meridional part of the Espinhaço Mountain Range (latitude 10–20°S). We sampled lizards in the mountaintop rocky field formation – above 1000 m a.s.l. (see Alves et al., 2014). Average monthly temperatures of the region vary from 17 °C to 24 °C, following a typical Cwb Köppen classification (see Alvares et al., 2013), with great daily variation in temperature.

2.2. Sampling procedures

We sampled lizards over three days from 9 to 11 November 2014, during the wet season. We searched for individuals by haphazardly walking through an approximately 40 ha area between 0900 h and 1600 h (local time, GMT-3), which corresponds to the peak of *E. nanuzae* activity (Filogonio et al., 2010). When lizards were sighted, we rapidly captured them by noose to avoid any bias in their body temperature due to behaviour disruption. To avoid a cooling effect on the lizards, we measured the body surface temperature of lizards within 20 s of capture. As body surface temperature of lizards relates to cloacal temperature (Bucklin et al., 2010), we considered our measurements of their surface temperature as a proxy of their body temperature (T_b). To eliminate bias from the cooling effect of wind on the exposed dorsal skin, the body temperature was measured on the ventral surface of lizards using a laser thermometer (Instrutherm TI-890, nearest 0.1 °C). To achieve this, we positioned the lizards so that ventral body surface of individuals was positioned 2 cm from the thermometer sensor's opening. This procedure ensured that the bodies of the lizards covered almost all of the thermometer's aperture. In addition, to guarantee no bias in the temperature record of the lizards due to the thermometer reading objects other than lizards, we took care to have no background object that could interfere with the thermometer sensor's reading. Each lizard was sexed based on the shape of the base of the tails (larger in males) and skin colouration (males develop conspicuous colour

patterns). Then, we measured their body size (snout-to-vent length, SVL) using a Vernier calliper (nearest 0.05 mm) and recorded their body mass using a spring dynamometer (nearest 0.25 g). To avoid pseudoreplication due to obtaining data on the same individuals, we marked the lizards with ink dots (Ferner, 2007). After these procedures, all animals were gently released at the site where they were first sighted. No animals were injured or killed during handling, and marked animals were observed to perform their behaviours without disruption during the ongoing field study. We were careful to only conduct samplings under similar sunny period weather conditions.

Soon after capturing the lizards, we measured the substrate temperature (T_s) using the laser thermometer. We also measured air temperature (T_a) with a pocket Kestrel™ weather meter (nearest 0.1 °C) by positioning the bulb (shaded) 1 cm above the location where the animal was first sighted, and the wind speed was also measured (5 cm above substrate) with a digital anemometer (nearest 0.1 m/s) at the same place. We also recorded the solar radiation in this location using an Instrutherm MES-100 solar radiation meter (nearest 0.1 W/m²).

2.3. Data analysis

We evaluated the effects of the abiotic factors and body mass on *E. nanuzae* T_b by using generalised linear models (GLM). For this, we assigned T_b as response variable and solar radiation, T_s , wind intensity, T_a , body mass, and sex as factors (Zuur et al., 2009). Hence, we compared five GLM models: Model I – without any interaction term between factors; Model II – interaction term between wind intensity and T_a ; Model III – interaction term between T_s and wind intensity; Model IV – interaction terms between T_a and wind intensity and also between wind intensity and T_s ; Model V – interaction term between T_s and T_a . Only adult individuals were used for the analysis due to constraints in sexing young individuals. All statistical procedures were performed in the R environment (R Core Team, 2017) using the lme4 (Bates et al., 2014), car (Fox and Weisberg, 2011), and MASS (Venables and Ripley, 2002) packages.

3. Results

We sampled 68 *E. nanuzae* individuals, 29 females (SVL: 54.82 ± 13.8 mm; body mass: 5.85 ± 1.25 g) and 39 males (SVL: 52.61 ± 12.3 mm; body mass: 4.99 ± 1.08 g). The T_b of the lizards followed a similar pattern of variation through the day to that of T_s , although T_s reached greater values than the T_b of lizards (Fig. 1, Table 1). On the other hand, T_a varied over time with lower values than the T_b of *E. nanuzae* (Fig. 1, Table 1). The mean T_b of females was 33.08 ± 2.26 °C while the mean T_b of males was 33.28 ± 3.50 °C. Model I performed best among the models tested (Table 2). According to this Model, sex did not affect *E. nanuzae* T_b ($P = 0.26$) (see Table 2). Moreover, Model I showed that wind intensity had a negative effect on T_b (Fig. 2a, Table 3), while T_s positively affected the T_b of lizards (Fig. 2b, Table 3). The body temperature of the lizards was not related to solar radiation, T_a , or their body mass ($P > 0.05$).

4. Discussion

We found the body temperature of *E. nanuzae* varied up to 12 °C and was affected by environmental conditions. The body temperature of the lizards increased as substrate temperature increased, whilst the body temperature of *E. nanuzae* decreased as wind intensity increased. In addition, our data showed that males and females had similar body temperatures.

Intersexual differences for body temperatures can be related to sexual dimorphism for body size (or body mass). In these cases, the sex with larger individuals will be that with larger thermal inertia, and differences in body temperatures between the sexes will be related to differences in the thermal inertia between males and females (e.g.

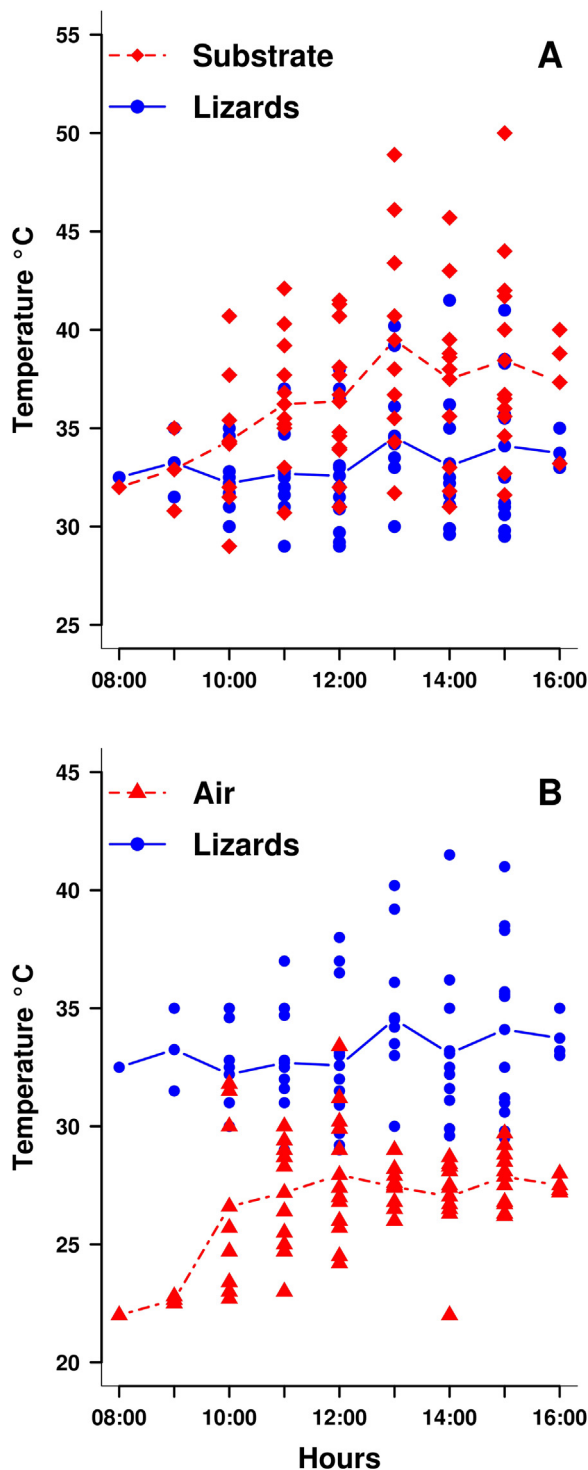


Fig. 1. Variation over time of body temperatures (blue circles and solid line), substrate temperatures (red diamonds and dashed line) (A), and air temperatures (red triangles and dashed line) (B) of the small-sized lizard *Eurolophosaurus nanuzae* from a mountain area of Serra do Cipó, Minas Gerais state, Brazil, through daily samplings. Symbols with lines represent the averaged values per hour of the correspondent variable.

Maia-Carneiro and Rocha, 2013). Nevertheless, male and female *E. nanuzae* did not present sexual body size dimorphism (Galdino et al., 2003), and thus one might expect similarities in thermal inertia between the sexes for the species. Hence, for *E. nanuzae*, similar body temperatures of males and females might be explained in the light of similarities in physiological requirements between the sexes imposed by

Table 1

Mean and standard deviation (SD), range, 95% confidence interval (CI), and standard error (SE) for body temperature (T_b), substrate temperature (T_s), air temperature (T_a), wind speed, and solar radiation experienced by the small-sized lizard *Eurolophosaurus nanuzae* ($n = 69$) from Serra do Cipó, Minas Gerais state, Brazil.

	Mean \pm SD	Range	95% CI	SE
T_b (°C)	33.2 \pm 3.01	29–41.5	32.48–33.91	0.36
T_s (°C)	36.88 \pm 4.49	29–50	36.16–37.59	0.54
T_a (°C)	27.24 \pm 2.35	22–33.4	26.53–27.96	0.28
Wind intensity (m/s)	1.58 \pm 1.49	0.0–5.6	0.86–2.29	0.18
Solar radiation (W/m ²)	859.69 \pm 426.18	15.705–1546.00	858.00–860.4	51.68

Table 2

Comparison of GLMM models on the effects of substrate temperature, solar radiation power, wind intensity, air temperature, and body mass (fixed effect variable) as well as sex (random effect variable) on the body temperature of the lizard *Eurolophosaurus nanuzae*. AIC = Akaike information criterion, BIC = Bayesian Information Criterion, df = degrees of freedom.

	AIC	BIC	df
MI: All independent variables without any interaction term	318.16	336.03	8
MII: with interaction term between air temperature and wind intensity	319.33	339.44	9
MIII: with interaction term between substrate temperature and wind intensity	319.84	339.95	9
MIV: with the interaction terms of MII and MIII	319.87	339.98	9
MV: with interaction term between air and substrate temperatures	321.14	343.49	10

similar body sizes. Alternatively, body temperature can be expected to differ between sexes due to differences in the social roles of males (territorial) and females (non-territorial). In a territorial and polygynic system, males have to engage in behaviours to maintain an area of exclusive use, such as patrolling and displaying against intruders (e.g. Baird et al., 1996; Jenssen et al., 2000). On the other hand, females in these systems do not have to perform social behaviours related to territoriality (e.g. Baird et al., 1996; Jenssen et al., 2000). Therefore, there may be a compromise between time allocated to performing social interactions and thermoregulation for males (Dunham et al., 1989) that does not occur for females. Males *E. nanuzae* are territorial (Quintana and Galdino, 2017) while females have not been observed acting territorially (Galdino, Pers. Obs.). Therefore, one could expect that the body temperature of *E. nanuzae* might differ between the sexes due to differences in the social role of males and females. However, our results show that the body temperatures of males and females lizards are similar, which indicates that our results cannot be explained in light of intersexual differences in social behaviours. Thus, our data corroborates the pattern of intersexual similarities of body temperatures for lizards as reported by Huey and Pianka (2007).

We found that the body temperature of *E. nanuzae* was affected by substrate temperature. On the other hand, the body temperature of individuals was neither influenced by solar radiation nor by air temperature. These findings stress the importance of the rocky substrate as a heat source for the species. Indeed, substrate temperature has been identified as an important thermal source for other iguanian lizard species (e.g. Kiefer et al., 2007; Ibargüengoytia and Cussac, 2002; Hatano et al., 2001; Bergalo and Rocha, 1993), and even for *E. nanuzae* when body temperature was measured using cloacal temperature (simple linear regression: $R^2 = 0.23$; $P = 0.02$, $n = 22$; Galdino unpublished data). Thermoregulatory behaviour can be influenced by the evolutionary history of lizards (Grigg and Buckley, 2013). Therefore, phylogenetic effects on the relationship found between body

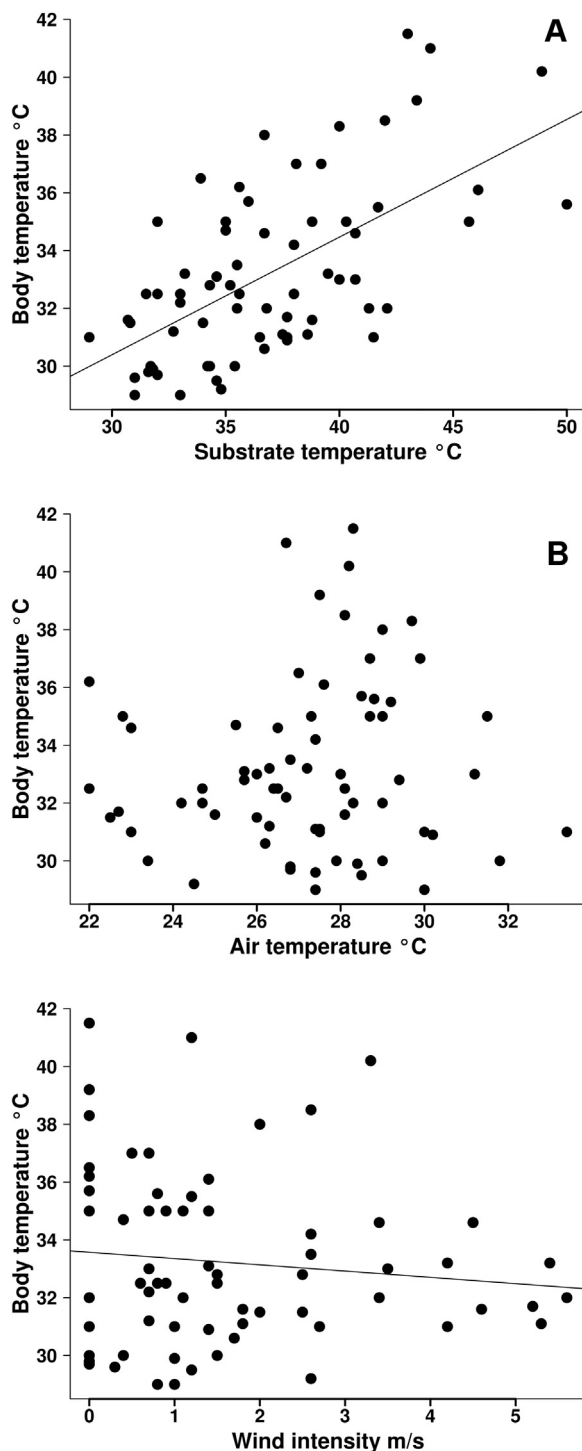


Fig. 2. Linear relationship between active body temperature and substrate temperature (A), air temperature (B), and wind intensity (C) of the small-sized lizard *Eurolophosaurus nanuzae*, inhabiting a mountain habitat in Serra do Cipó, Minas Gerais state, Brazil.

temperatures and substrate temperatures for iguanian lizards cannot be disregarded. Nevertheless, one might consider our results may be biased as our measurement of body temperature corresponds to the ventral part of lizards, leading T_b to be more related to substrate temperature.

Tropidurid lizards are considered as heliotherms, using solar radiation as the main heat source (e.g. Albuquerque et al., 2018). However, our results show that *E. nanuzae* body temperature is unrelated to

Table 3

Summary of the statistics and coefficients of the fixed effects from the best GLMM tested model regarding the influence of substrate and air temperatures, wind intensity, solar radiation, and body mass of *Eurolophosaurus nanuzae* on their body temperatures. Degrees of freedom = 1.

Factor	Estimated	Standard error	t Value	χ^2	P
Substrate temperature	0.46	3.97	7.03	49.35	< 0.001
Air temperature	-0.16	1.29	-1.24	1.54	0.99
Wind intensity	-0.63	7.65	-2.97	8.84	0.003
Solar Radiation	< 0.001	0.066	0	0	0.14
Body mass	0.33	0.22	1.48	2.20	0.22

solar radiation but is positively related to substrate temperature. Thus, rocks, and not solar radiation, seems to be the main heat source for the tropidurid lizard *E. nanuzae*, and the species might be considered as tigmothermic. Nevertheless, a potential bias from the effect of substrate temperature on the body temperature of lizards (see above) might be considered.

Moreover, it should be noted that *E. nanuzae* inhabits open rocky outcrop habitats where rocks, the substrate used by the species (Kiefer, unpub. data), can reach far higher temperatures than the body temperature of *E. nanuzae*, as our results show. Hence, using rocks as a heat source can restrict the activity time for the species as individuals might avoid the hotter period of the day, which in turn, could impose physiological risks of death if no other factor influences an individual's body temperature. Furthermore, it is important to highlight that *E. nanuzae* is a small-sized species whose body size reaches a maximum of 6 cm with a mean maximum body mass of approximately 5 g, and thus they have a large surface area to body volume ratio. A larger surface to volume ratio can facilitate the rapid warming of lizards, putting the individuals at risk of overheating if no mechanism exists to provide an efficient control of body temperature. Therefore, *E. nanuzae* individuals are expected to have an efficient thermoregulatory mechanism.

However, it is important to consider the negative relationship between wind intensity and body temperature for *E. nanuzae*. Other studies also found wind speed was negatively related to the body temperatures of lizards, such as for *I. Aurelioi*, a lizard species inhabiting a high-elevation mountain environment (Ortega et al., 2016b). For *I. aurelioi* winds were suggested to reduce body temperatures through direct convective cooling of lizards, and also indirectly via the convective cooling of the substrate (Ortega et al., 2016b), and thus constraining the thermoregulation of lizards. Furthermore, the body temperature of *Liolaemus lutzae* was constrained by wind intensity during the cooler period of the year (Maia-Carneiro et al., 2012). Therefore, the studies up to now have indicated that wind is a constraining factor for thermal biology of lizards (see also Logan et al., 2015). We did not find that winds exerted a prompt convective cooling effect on the rocky substrate (Simple linear regression: $R^2 = 0.04$; $P = 0.09$), which we relate to the high thermal inertia of the rocks. It is important to mention that, in the studied site, rocks are the dominant substrate (Vaclav and Galdino in prep.), which implies a large availability of hot substrates. We suggest that, in the studied system, lizards might be using wind to counterbalance the heat they are exposed to from the rocky substrate through convective cooling of their body's surface. Hence, contrary to previous studies (e.g. Ortega et al., 2016b; Logan et al., 2015; Maia-Carneiro et al., 2012), the small-sized *E. nanuzae* should benefit from the effects of cooling winds. Thermoregulation of *E. nanuzae* might thus involve a mechanism in which the potential risks imposed by high substrate temperatures can be offset by exposure to cooling winds. Consequently, due to the large availability of heat sources (rocks) and the potential for lizards to overheat on a hot rocky substrate, we suggest that good thermal sites for *E. nanuzae* might be those with an appropriate incidence of winds to enable individuals to cool.

However, an exposure to wind might be accompanied by costs. Studies have shown that wind exposure can impair communication of

lizards (Peters et al., 2007), increase bodily water loss (Waldschmidt and Porter, 1987), and decrease activity (Logan et al., 2015). Hence, a trade-off can be expected between the thermal benefits of the winds and the associated physiological and/or behavioural costs.

Finally, lizards are expected to be impacted by climate change. In a scenario of warmer temperatures, individuals are expected to seek shelter to cool their body temperatures during a large part of their daily activity (Huey et al., 2012). This will limit the time lizards have to forage, thus constraining the energy stocks they allocate to reproduction (Huey et al., 2012). Neotropical lizards face risks of extinction as a consequence of warmer temperatures (Sinervo et al., 2010), and South America is indeed expected to experience an increase of 2–6 °C in the range of air temperatures (Salazar et al., 2007). However, the effects of global change on Neotropical mountain lizards are poorly known. Currently, the knowledge on thermal biology of mountain lizards is based on studies of species living in temperate environments. In temperate environments lizards are adapted to live under cold conditions. Global warming can increase the temperatures of mountain environments and threaten lizards that are cold specialists as environmental temperatures rise, the constraints they will face will be greater than they are adapted to. On the other hand, mountain lizards from tropical environments are not cold specialists, and therefore, they might face different threats from global warming compared to lizards from temperate mountain habitats. We suggest that *E. nanuzae* individuals have the need to use a cooling source to avoid their body temperatures overheating from the substrate. Therefore, the challenge for tropical mountain lizards under global warming might be related to the avoidance of warmer environmental temperatures. As predicted by Huey et al. (2012) this might lead lizards to restrict their time of activity, which can be a major constraint if no alternative cooling source is available for them, as air temperatures are expected to increase.

5. Conclusions

Our results highlight the importance that Ortega et al. (2016b) attributed to the role of winds on the thermal biology of lizards. Wind can affect lizards, constraining their thermal environment and limit thermoregulation through cooling effects. Nevertheless, our results are consistent with the cooling effects of winds improving the thermoregulation of lizards living in hot surface environments. Therefore, we suggest wind as an important condition used by the lizard *E. nanuzae* to actively regulate their body temperature.

Acknowledgements

We thank the administrative staff of Reserva Vellozia and G. W. Fernandes for permission to work in the area. We are grateful to S.P.R. Ventura and G.C. Melo for help in the field. A.S.B. Gontijo thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES); A.F. Righi and C.S. Garcia thank Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for the student fellowships.

Conflicts of interest

None.

Funding sources

Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG), Brazil.

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (FAPEMIG), Brazil – CAPES.

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